THE RHEOTROPISM OF ROOTS.

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(WITH FIFTEEN FIGURES)

[*Continued from p. 198.*]

II. VELOCITIES EFFICIENT IN THE FORMATION OF CURVES.

IN my published abstract,[1] already referred to, it was stated that definite relations exist between the velocity of flow and the response of the root. Juel[2] paid some attention to the same subject, finding that *Vicia sativa* grew generally with a negative curve, or straight, in velocities above 1800^{cm} per minute; while from that rate down to 1.8^{cm} per minute the response was generally a positive curve. Similarly with *Zea mays* (the variety is not given), the same author found devious behavior in a velocity of 3000^{cm} per minute, but positive curves in a velocity of 1200^{mc} per minute; in velocities of 66^{cm} to 18^{cm} per minute, he found 67 per cent. curved positively; while in velocities of 4.8^{cm} to 1.8^{cm} per minute, less than one-half the roots bent positively. It is clear, therefore, that in a velocity above 1800^{cm} per minute, the primary roots in both species named grow either straight or with a negative bend. As Juel points out, this does not necessarily mean that the roots are either insensitive or negatively rheotropic. They are probably bent negatively or held vertical by the mechanical push of the water. On the other hand, the lower limit of a stimulating current seems to have been approximated for *Zea mays*, but not for *Vicia sativa*, at the rate of 2^{cm} per minute.

My own experiments to determine the limiting velocities inducing response have been carried on with several plants, but

[1] Rheotropism and the relation of response to a stimulus. BOT. GAZ. 22:242. 1896; Proc. Amer. Ass. Adv. Sci. 1896.

[2] JUEL: Untersuchungen über den Rheotropismus der Wurzeln. Jahrb. Wiss. Bot. 34:507. 1900.

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more extensively with *Zea mays* (popcorn), *Brassica alba*, and *Raphanus sativus*. While the general results could be given in a few words, yet, to afford the reader opportunity to judge the evidence, the following tables are given.

TABLE I.

EXPERIMENTS WITH ZEA MAYS (popcorn). Temperature in air 24°.

No. of experiment and revolutions per minute	Flow per minute	After 9¾ hours	After 18 hours
I 8 seedlings × 40	2500 to 500cm	8 roots = 0°	8 roots = 0°
II 9 seedlings × 26	1630 to 1300cm 1140 to 325	3 roots = 0° 6 roots = +15° to 40°	3 roots = 0° 6 roots = 0
III	1000cm	1 root = 0°	1 root = −90°
	900	1 root = 0	1 root = −45
	800	1 root = 0	1 root = 0
	700	1 root = +10	1 root = +10
8 seedlings × 16	600	1 root = +20	1 root = +25
	500	1 root = +20	1 root = +45
	400	1 root = +30	1 root = +60
	300	1 root = +40	1 root = +90
IV	125cm	1 root = +40°	1 root = +80°
	113	1 root = +45	1 root = +80
	100	1 root = +45	1 root = +45
	88	1 root = +35	1 root = +80
9 seedlings × 2	75	1 root = +40	1 root = +60
	62	1 root = +45	1 root = +45
	50	1 root = +45	1 root = +50
	38	1 root = +45	1 root = +60
	25	1 root = +45	1 root = +50

The results recorded in the foregoing table were all obtained with seedlings of the same planting; the experiments were carried on at the same time, at the same temperature, and in the same room. The external conditions, therefore, were as nearly alike as possible.

An examination of my notes on experiments performed at various times during the past three years shows that *Avena sativa* has varied in its response according to the velocity of the flow. Unfortunately, the experiments not being made for the purpose of determining the effect of various velocities, the notes were not taken in sufficient detail to show more than very general relations. The results are these :

TABLE II.

EXPERIMENTS WITH AVENA SATIVA. Temperature in air 22° to 25°; period for each velocity from 10 to 17 hours, except in the case of 15 roots, where it was 30 hours.

Total no. of roots	Flow per minute	Percentages of curvatures
96	25 to 100cm	46% = +, 51% = 0, 1% = −
57	100 to 300	81 = +, 14 = 0, 5 = −
58	300 to 2000	40 = +, 30 = 0, 30 = −

From this table it is evident that streams with a velocity below 100cm per minute do not bring responses in the majority of individuals; and that velocities of 2000cm and below give many negative curves, these probably being merely mechanical. It is quite probable that velocities above 300cm per minute would give a majority of positive responses, but my notes do not set the approximate upper limit.

The tests with *Brassica alba* show practically the same result as with *Avena sativa*. A velocity above 1000cm per minute will give, so far as my test goes, only vertical and negatively bent roots, while a velocity between 600cm and 1000cm per minute will not bring a positive response in one-third of the roots.

TABLE III.

EXPERIMENTS WITH BRASSICA ALBA, to show upper limit of speed calling forth a response.

Total no. of seedlings	Temperature in air	Period	Flow per minute	Percentage of curvatures
62	22° to 24°	15 to 24 hours	50 to 500cm	87% = +, 13% = 0°, 0% = −
32	22 to 23	14 to 24	600 to 1000	28 = +, 50 = 0, 22 = −
8	23	14	1000 to 2000	0 = +, 50 = 0, 50 = −

The table fails to show the various angles assumed by the roots in various velocities. In the rates between 100cm and 500cm per minute, the angle was in more than half the roots between 60° and 90°. In 56 seedlings tested in a velocity below 100cm per minute, the angle attained averaged less than 40°. In velocities above 600^{cm} per minute, the angle was less than in the lower rate.

The lowest speed to which any of the roots will respond with well-marked curves has been determined in another series of experiments. The same general method was used as before, except that a klinostat gave the revolution, and no seedlings were set nearer than 3^{cm} to the center of the dish. The seedlings were thus suspended across the diameter of the basin in four groups, two being in the outer circular channel 45^{mm} in radial width, and two being in the inner channel 35^{mm} wide, there being an unoccupied central portion of water 55^{mm} in diameter. The innermost roots that were 3^{cm} from the center were therefore within 5^{mm} of the inner glass wall, and hence it may be assumed that the friction of the water on the glass wall would maintain there a water current with fairly constant direction, even in this slow movement.

In the following table the roots are grouped in two classes—those in the outer channel of the revolving basin where there was a velocity of 2.36^{cm} to 4^{cm} per minute, and those in the inner channel where the velocity was 1.18^{cm} per minute to 2^{cm} per minute.

TABLE IV.

EXPERIMENTS WITH BRASSICA ALBA, to show the lower limit of speed calling forth a response.

EXPERIMENTS	VELOCITIES = 1.18^{cm} TO 2^{cm} PER MIN.						VELOCITIES = 2.30^{cm} TO 4^{cm} PER MIN.					
	No. of seedlings	% +	% o	% −	Average size of + angles	Extremes of + angles	No. of seedlings	% +	% o	% −	Average size of + angles	Extremes of + angles
I. 22° C., 23 hrs., × 1 in 16 min.	4 = + 3 = o°	57	43	o	24°	10° to 45°	8 = + 1 = o°	89	11	o	36°	10° to 45°
II. 22° C., 18 hrs., × 1 in 16 min.	4 = + 3 = o° 5 = −	33	25	42	29°	15° to 45°	14 = + 3 = o°	82	18	o	37.5°	10° to 45°
Total	8 = + 6 = o 5 = −	42	32	26	26°	10° to 45°	22 = + 4 = o°	85	15	o	37°	10° to 45°

The foregoing table does not tell the whole story. The roots in the velocities above 2^{cm} per minute had the characteristic appearance of rheotropic responses, the apical part of the root being bent in a curve. The roots in velocities below 2^{cm} per minute showed mere *inclinations* and not curves. Moreover, the bent roots in the higher velocity were in 80 per cent. curved only in a plane parallel with the current, while nearly all the bent roots in the lower velocity were curved either in planes oblique to the direction of the current, or they grew in two or more planes at various angles with one another. In other words, the *velocities below* 2^{cm} *per minute ceased to control the direction of growth.*

The fact last mentioned is further emphasized by the behavior of the roots of *Brassica alba* in basins of water revolving once in 24 minutes. With such a speed as this, the velocity in the outer channel of the basin extends from 2.50^{cm} to 1.80^{cm} per minute, and in the inner channel from 1.50^{cm} to 0.78^{cm} per minute. The behavior of the roots was about the same in both channels. Seventy-eight roots were used, the temperature being maintained constantly at 22° in air, and the period being 9 hours, 15 hours, 24 hours, and 28 hours in four experiments. Twenty-two roots inclined against the stream, fifteen with the stream, and forty-one roots were neutral. This gives 28 per cent. positive, 19 per cent. negative, and 53 per cent. neutral. But it would be unfair to regard these proportions as of much moment. Rather should it be said that the lower limit of velocity effecting positive responses on the part of these roots has been passed. It cannot be said, however, that the stream is wholly without influence on the direction of growth. Two-thirds of the mustard roots in velocities below 2^{cm} per minute deviated from the vertical direction in their growth. For purposes of summarizing the results given above, all roots bent from the vertical plane in which the seedlings were suspended were counted as either positive or negative, and all roots remaining in this plane were counted as neutral; but many of the roots counted as positive or negative were also oblique to the direction of the current, and many counted as neutral deviated from a straight course. That this very irregular direction of growth in streams of low speed is due to the movement of water is made known from the fact that these seedlings produce very straight roots in still water. In a control test, fifteen seedlings suspended with their roots in still water grew straight. It seems to be demonstrated, therefore, that currents of water with a velocity less than 2^{cm} per minute are not able to call forth a positive response in the primary root of *Brassica alba*.

The results obtained in attempting to determine the minimum, optimum, and maximum velocities for inducing a rheotropic response in *Raphanus sativus* show that this plant agrees very closely in these respects with *Brassica alba*. Since these results can be most briefly given in tabular form, we will again resort to that method of presentation.

TABLE V.

EXPERIMENTS WITH RAPHANUS SATIVUS, showing relation of response to velocity. Period, 8 to 24 hours, the record being made when the most curves showed in each experiment.

Total seedlings	Temperature in air	Flow per minute	Percentage of curvatures		
36	22 to 24°	25 to 100^{cm}	72 % = +	28 % = 0	0 % = −
117	22 to 24	50 to 500	93 = +	3.5 = 0	3.5 = −
24	23	600 to 1000	12.5 = +	87.5 = 0	0 = −
10	22 to 23	1000 to 2000	0 = +	40 = 0	60 = −

From this table it appears that approximately one-fourth of the roots remain neutral in a velocity between 25^{cm} and 100^{cm} per minute, that the optimum speed lies between 50^{cm} and 500^{cm} per minute, and that velocities above 1000^{cm} per minute will not call forth a positive response. This table, however, is not a precise statement of the percentages of response, since some roots curved and straightened again before the final record was made. Such roots were very few in number, and it is not probable that the percentages would be changed more than one or two units if the more accurate record were made.

Not only is the largest number of positive curvatures obtained in velocities between 50^{cm} and 500^{cm} per minute, but the largest angles also. The most of the curves in velocities below 50^{cm} per minute are less than 30°, while the greatest angles are attained in velocities between 200^{cm} and 500^{cm} per minute.

To determine the effect of a very slow current on the direction of growth of the roots of *Raphanus sativus*, three experiments have been carried out with the revolving water basin, divided as before into three concentric compartments, the roots being immersed in the two outer. The klinostats were adjusted to give one revolution in 32 minutes and one in 45 minutes, offering velocities ranging from 0.4^{cm} to 2^{cm} per minute. No difference in behavior of roots could be detected for the various velocities. The temperature of the air was held constantly at 23°; the period of two experiments was 22 hours, and the other 24 hours. Altogether seventy seedlings were used, giving thirty-four positive inclinations and three negative, while thirty-three roots grew straight.

In the first place, it may be said that the roots of Raphanus are not disturbed, as are those of Brassica, by the very slow currents of water. It will be recalled that two-thirds of the roots of the former grow irregularly in direction, in streams with a current below 2^{cm} per minute. The roots of Raphanus, which are designated above as neutral, pursued a vertical course downward.

In the second place, the fact should be emphasized that in these slow streams the character of the bend of the roots is different from that seen in the higher velocities. In the latter a positive curve is concave toward the stream; in the former the inclination against the stream is either convex toward the stream, or the inclination is in a straight line. In very weak currents, below 2^{cm} per minute, the apex of the root for 2^{mm} or 3^{mm} points vertically downward. The accompanying *fig. 8* will illustrate this difference. The angles attained by the roots of *Raphanus sativus* in these very low velocities ranged from 10° to 45° from the vertical.

Seeing that nearly all the bending roots of the radish are turned against the stream, we must name the phenomenon positive rheotropism, even in velocities below 1^{cm} per minute. The case is different with the mustard. In that plant velocities below 2^{cm} per minute gave only 28 per cent. of obliquely positive inclinations to 19 per cent. of negative, and 53 per cent. of neutral roots. The difference between the number of positive and negative roots in the mustard is not so great that we may call the excess of 9 per cent. indicative of a positive response. With the radish, however, the roots bend only in a plane parallel with the stream, and thirty-four positive roots to three negative and thirty-three neutral require the verdict that approximately one-half the roots of *Raphanus sativus* are directed by a water stream with velocities ranging from 0.4^{cm} to 2^{cm} per minute, or even by a velocity of less than 1^{cm} per minute.

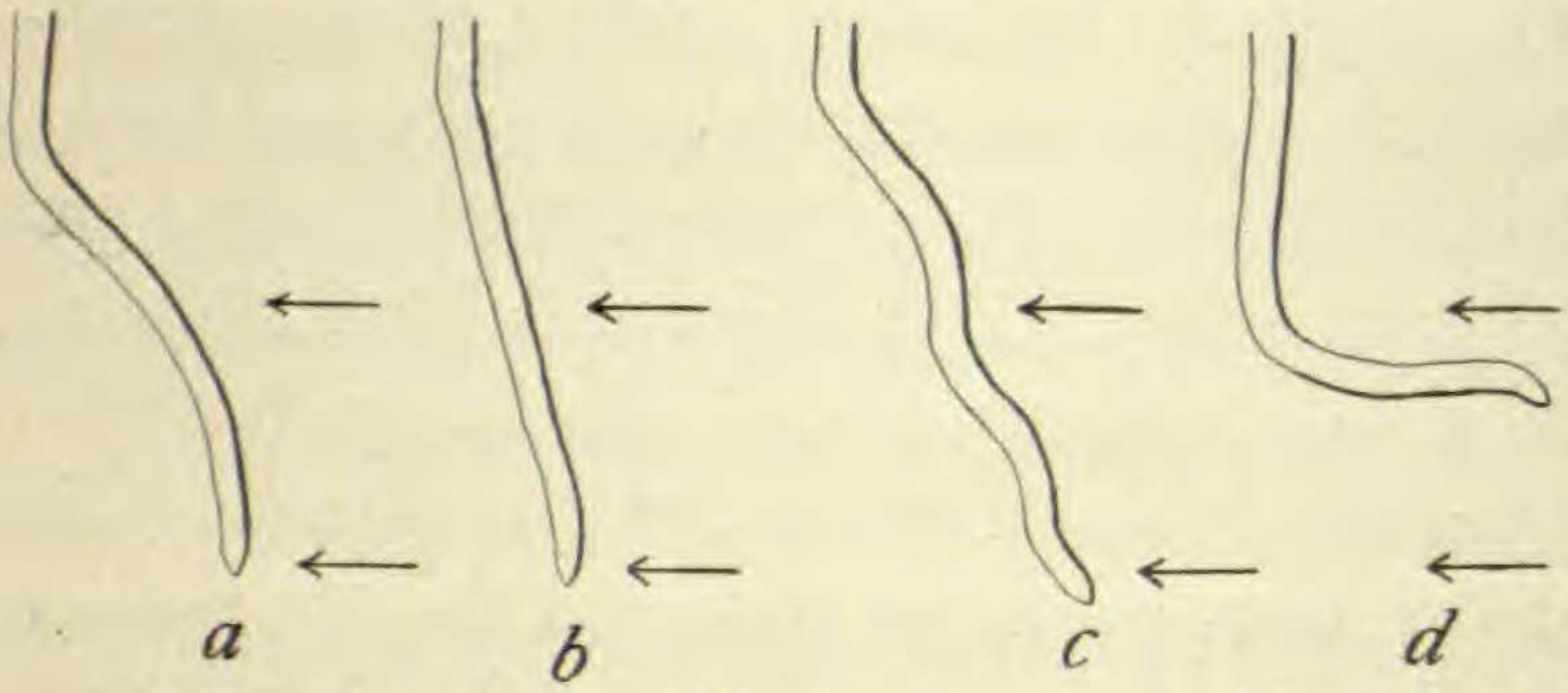

FIG. 8.— Four roots of *Raphanus sativus* after stimulation by the water current. Roots *a*, *b*, and *c* have been in streams with a flow of less than 2^{cm} per minute, while *d* has been in a stream of 200^{cm} per minute.

Helianthus annuus gives mostly positive responses in velocities from 100^{cm} to 600^{cm} per minute; while in one experiment with six seedlings, velocities from 600^{cm} to 2500^{cm} per minute, one root was positive, four negative, and three neutral. *Pisum sativum* in three experiments, with velocities from 500^{cm} to 1400^{cm} per minute, gave nine positive roots, sixteen negative, and nine neutral. From this we may infer that the higher velocities at least cause mechanically negative bends.

Vicia faba gives positive curves in a stronger stream than any other plant worked with. In one experiment, with velocities from 600^{cm} to 2500^{cm} per minute, eight roots bent positively, eight negatively, and three were neutral. In another experiment with six seedlings, two were neutral, while four were positive—one at 1000^{cm} velocity, one at 1500^{cm}, and two at 2000^{cm}.

This is the only plant that has not always given a negative bend in a velocity of 2000^{cm} per minute.

An examination of my notes on all experiments shows that, without having determined the optimum velocity precisely for any species, all of the plants I have worked with give the most constantly positive responses and attain the greatest angles in velocities between 100^{cm} and 500^{cm} per minute.

III. LATENT PERIOD AND AFTER-EFFECT.

A remarkable fact in the rheotropic response of roots is the extraordinarily long latent period. It is true that Berg[3] states that he obtained curves often within thirty minutes. But he gives neither the precise plants, nor temperature, nor velocity with which this result was obtained. When he used the reading microscope in an experiment with *Zea mays*, he found a minimum latent period of one hour. Juel (*l. c.*, p. 529), with *Vicia sativa*, temperature and velocity not given, believed he could detect initial curves in two hours.

My own results agree with those of Berg and Juel, but they have been extended over a larger number of plants, and have brought in also the relation of velocity of current to time of response. The following tables will show how these plants have behaved. Observations were made at the intervals recorded in the tables; and hence the curvatures recorded for any hour, except the first, may have begun between the time recorded and the preceding observation. Close attention failed to reveal any curvature earlier than eighty minutes. Observation was made with the unaided eye, and we may assume, therefore, that the reading microscope would have shown a shorter latent period than eighty minutes. Reference to *fig. 10*, page 275, will convince one that several of those curves must have begun at least ten to fifteen minutes earlier than the time recorded.

The mark "?" in the following table indicates that no observation was made at that time.

[3] BERG: Studien über Rhetropismus. Lunds Universit. Årsskr. 35[2]: no. 6. 1899.

TABLE VI.

LATENT PERIOD FOR RAPHANUS SATIVUS.

Flow per minute	Temperature in air	Number seedlings	Behavior after 1½ hours	2 hours	2½ hours	3 hours	4 hours	4½ hours	6 hours	7 hours	10 hours	Total no. showing curves within 24 hours
25- 50cm	23°	3	0	0	0	0	0	0	0	0	0	0
60- 100	23	9	0	0	0	0	0	3+	3+	4+	4+	4+
125- 200	23	9	0	2+	2+	3+	3+	3+	5+	?	?	9+
225- 400	23	5	1+	2+	2+	2+	2+	3+	4+	?	?	5+
	26	10	1+	1+	1+	1+	5+	7+				7+
425- 750	23	12	8+	8+	8+	8+	8+	8+	8+	?	?	[illegible]
	26	14	4+	4+	7+	7+	8+	8+				8+
775-1500	23	20	0	0	0	0	0	0	3+	3+	?	7+
1525-2500	23	5	0	0	0	0	0	0	0	0	?	1+

The following table shows the shortest latent period observed for several seedlings. It is certain that the latent period would not be shorter in a velocity either less or greater than that given for each plant, with the exception of that for *Brassica alba*. For this plant, experiment has not shown whether a quicker response would be found in a velocity greater than 250cm per minute.

TABLE VII.

SHOWING SHORTEST LATENT PERIOD OBSERVED FOR SEVERAL PLANTS.

Plants	Optimum temperature for growth [4]	Temperature of air in experiment	Flow per minute	Latent period
Raphanus sativus	——	23°	200–400cm	1½ hours
Brassica alba	27.4°	23	200–250	2
Hordeum vulgare	28.7	23	100–225	2
Avena sativa	——	23	100–225	2½
Zea mays (popcorn)	33	24	200–400	3
Pisum sativum	25	23	200–600	3½
Helianthus annuus	31.5	23	150–300	3½
Vicia faba	26.6	25	225–675	6

Lathyrus odoratus responds so slowly that in a set of twenty seedlings in a favorable velocity of water, at a temperature of 20° to 23°, 24 hours elapsed before I was certain that the roots were responding; yet within the next 24 hours fourteen roots showed good rheotropic curves.

[4] These temperatures are taken from the tables in Sachs' *Text-book of Botany*, translated by Vines, 1882, p. 830, but are changed in two cases to accord with results obtained in my own work.

A comparison of the optimum temperature for growth with the temperature used in the experiments will indicate that the seedlings used would probably, in most cases, show in the optimum temperature a shorter latent period than that given.[5] We may suppose that by the aid of the reading microscope the latent period could be seen at the optimum temperature to end for *Raphanus sativus*, *Brassica alba*, and *Hordeum vulgare* in an hour. It is hardly to be supposed, however, that for *Pisum sativum*, *Lathyrus odoratus*, and *Vicia faba*, the latent period could be reduced to two hours. Compared with the latent period in geotropic response, the periods for rheotropism are extremely long. The roots of *Raphanus sativus* when laid horizontally in water, at a temperature of 26°, show to the unaided eye a geotropic bend in 15 minutes; those of *Pisum sativum*, similarly treated, show, at a temperature of 23°, a geotropic bend in 20 minutes. The latent period for rheotropism, therefore, is six times as long as that for geotropism. A rheotropic curve, however, is carried out in opposition to the geotropic tendency of the plant. No one has yet found the latent rheotropic period when gravitation is neutralized. A better comparison can be made with the heliotropic latent period, which is shown by the plant while still under the influence of gravitation.

If seedlings of *Brassica alba* and *Helianthus annuus* have their roots immersed in water in an air temperature of 23°, and are then exposed to one-sided illumination with strong, diffused light, their latent period will be found comparable to that in rheotropism. Four seedlings of *Brassica alba* were used, and the first negative bend perceptible to the naked eye came in 75 minutes. Within two hours of the beginning, all four roots had strong negative curves. The heliotropic curves in Helianthus did not appear until 2½ hours had elapsed; then only three roots out of five had responded.

Tables VI and VII also show the latent period in relation to the velocity of flow. In general, it may be said that for several

[5] CZAPEK (Jahrb. Wiss. Bot. 32: 195) shows that the optimum temperature for growth gives the quickest geotropic response.

plants the latent period is shortest in velocities between 100cm and 400cm per minute. *Raphanus sativus* and *Vicia faba*, however, have shown their shortest latent period in velocities above 400cm and below 750cm per minute. The influence of velocity on the time of response is shown in a striking way by using the basin of water, revolving at a rate to give critical velocities in the radius, and by suspending a row of seedlings along the radius. From scores of such experiments, two may be selected here. In the first, the revolution was twice to the minute, giving along a radius velocities from 25cm to 125cm per minute. The temperature in water was 22°, and twelve seedlings of *Raphanus sativus* were employed. In two hours the three outermost seedlings had bent + ; in three hours the three outermost were + ; in four and one-half hours the six outermost were + ; and in seven hours the seven outermost were + , while the remaining five nearer the center were all neutral. In the second selection, seedlings of *Brassica alba* were used. The temperature in water was 23°, the revolution 24 times to the minute, and the velocities ranged from 300cm to 1500cm per minute. After three hours the three roots nearest the center of the basin were + ; after eight hours the six nearest the center were + ; and after fifteen hours the eight nearest the center were + ; while the fourteen outermost were all directed vertically downward and therefore to be called neutral.

The foregoing considerations have shown us that the time of response stands in definite relations to the velocity of current. We may at this point inquire whether the variation in the time of response in constant external conditions may be referred wholly to variation in the rate of growth. A seedling is usually regarded as so low an organism among organized beings, that one might expect a low degree of individualization, one might expect constant results in constant conditions of growth and environment. Could we not carry on our experiments in rheotropism quantitatively, and thereby look for constant latent periods and constant angles? The experience of every botanist is against such an assumption. Every one is familiar with the fact that when several seedlings have their roots laid horizontally so as to carry out the geotropic curve, some roots bend at angles varying from those of the majority, indicating either an individualism in sensitiveness or in response. The rheotropic response shows like variation. In general, the most rapidly growing roots are the first to respond, but in nearly every experiment there are found roots varying their time of response from that of their fellows of equally rapid growth. This fact is illustrated by *figs.* 9 and *10*. It is easy to see that root no. 5 has grown most and also curved most; but root no. 2 has grown less and bent more than no. 1, and no. 6 has grown less and bent more than no. 7. It is true that in these cases external conditions were not precisely similar, for the velocity of current for some of the roots was 675^{cm} and for others 725^{cm} per minute, disregarding the irregularities of current caused by the roots themselves. However, root no. 2 was in almost exactly the same theoretical rate of flow as no. 4, must have felt more of the irregularity of flow caused by the roots in front of it than did no. 4, and grew less than no. 4; yet it curved to a greater angle. On the other hand, many of these variations in physiological reaction could probably be reduced were care taken in selecting individuals whose past development and history were known to be similar.

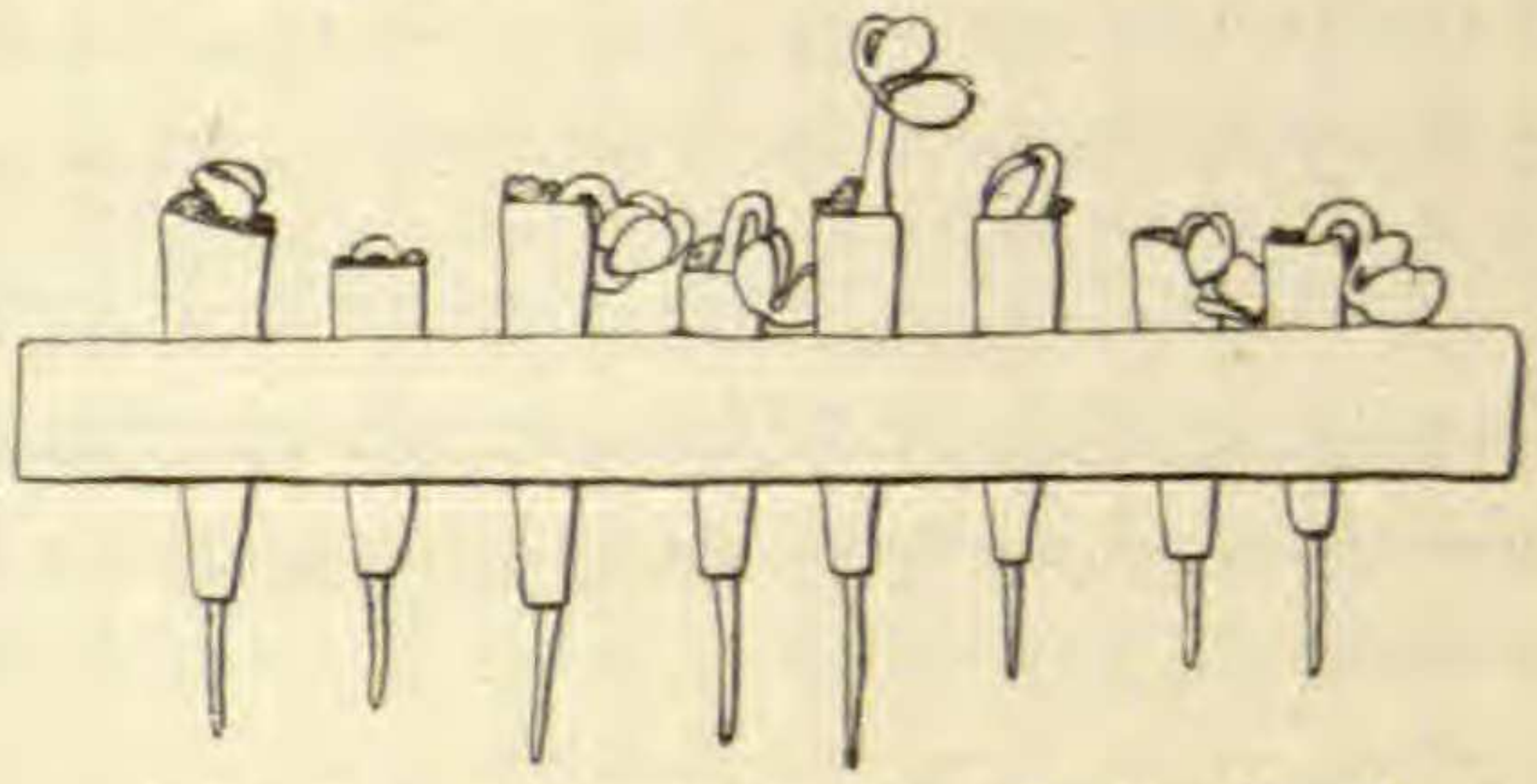

FIG. 9.—*Raphanus sativus*, tracing from a photograph. Seedlings ready for the experiment whose result is shown in *fig. 10*.

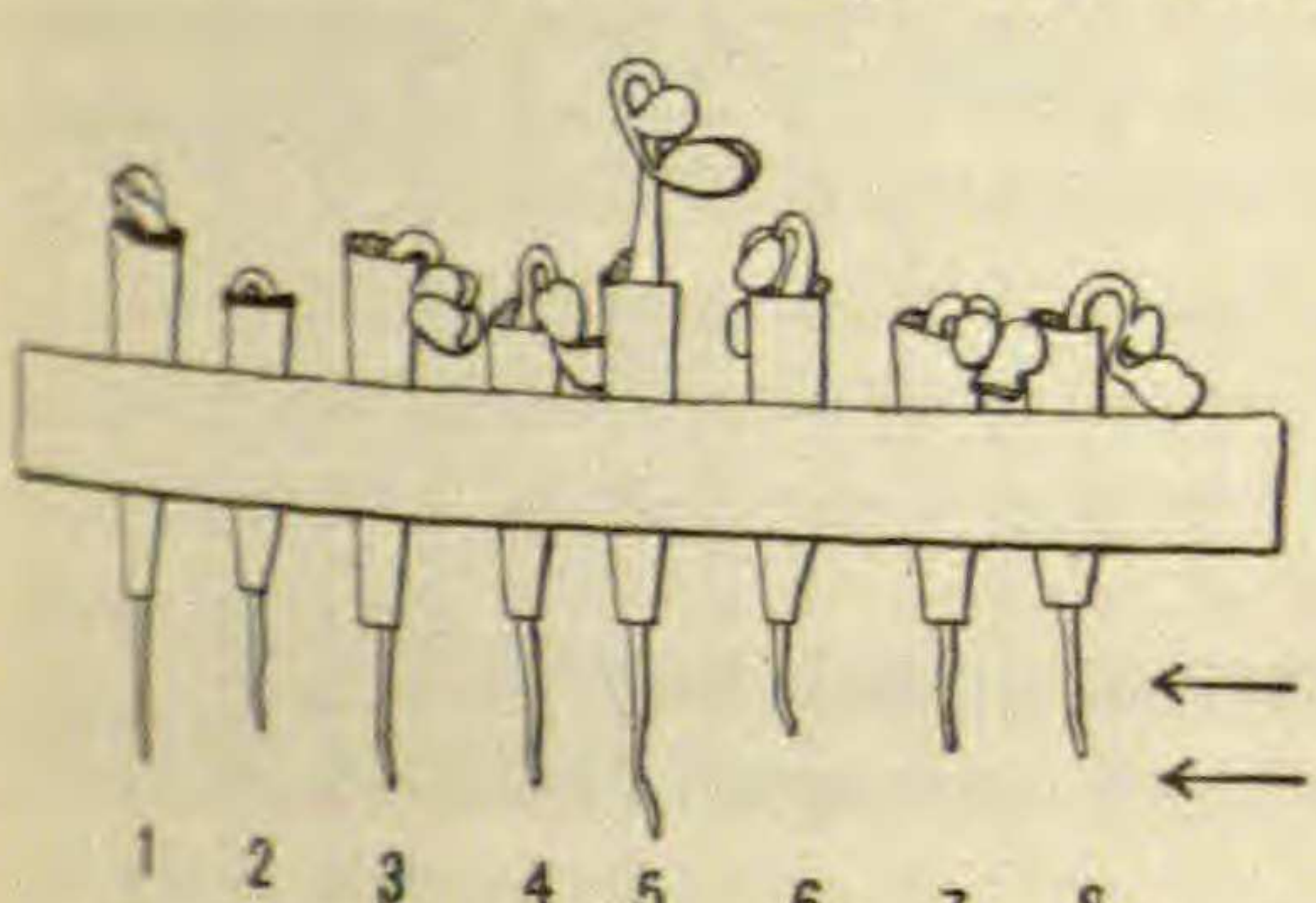

FIG. 10.—*Raphanus sativus*, traced from a photograph taken 1½ hours after placing the roots in a water stream with a temperature of 21°, and a velocity of 675^{cm} to 725^{cm} per minute. To show initial rheotropic curves.

The after-effect of the rheotropic stimulus is shorter than the rheotropic latent period, both considered without the neutralization of the effect of gravitation. Roots of *Raphanus sativus* rheotropically curved have been seen to begin to straighten geotropically 20 minutes after the water stream was stopped, the temperature in air being 23°. Under similar conditions, except at an air temperature of 28°, the roots of *Zea mays* (*everta*) began to straighten geotropically in 40 minutes. On the other hand, two roots of *Vicia faba*, at a temperature of 25° in air, continued to bend rheotropically for an hour after the water stream was stopped.

From the foregoing results we may conclude that the rheotropic stimulus is in active competition with the geotropic stimulus, so that the operation of the latter is very quickly manifested when the former ceases to operate. One might have supposed the after-effect would have been considerably protracted, seeing that the latent period is so long. Such, however, is not the case. It remains an open question whether the rheotropic latent period would be greatly shortened were the opposing geotropism eliminated. The latent period in this response is no greater than that for traumatropism [6] and that for the clasping of some tendrils.[7]

IV. PERSISTENCE OF SENSITIVENESS.

The response of roots to a stream of water is continuous over a long period; and although there is some evidence to show that roots subjected to a rheotropic stimulus lose in great measure their geotropic sensitiveness, yet we may regard the direction taken by the roots growing in a stream of water as a resultant direction. This resultant direction forms a greater or less angle with the vertical according to the plant species, and according to the intensity of the rheotropic stimulus. This angle may reach 90° in *Fagopyrum esculentum*, *Raphanus sativus*, *Brassica alba*, and other plants, or it may average no more than 45° as in *Vicia faba*, *V. sativa*, *Pisum sativum*, and *Helianthus annuus*. A very weak

[6] SPALDING: On the traumatropic curvature of roots. Annals of Botany 8: 427.

[7] DARWIN: The movements and habits of climbing plants. London. 1875.

stimulus, such as that given by a water current of a few centimeters per minute, gives an average angle in *Brassica alba* and *Raphanus sativus* of perhaps 15°, while the most favorable stimulus brings a response averaging nearly 90°.

It might be thought that a root responding to the rheotropic stimulus by producing an angle of 45° to 90° from its direction of geotropic equilibrium would soon show signs of fatigue by the reduction of this assumed angle. Such behavior, however, on the part of the plant has not been observed, in cases where the stimulus is above a relatively low intensity and below a relatively high mechanical pressure. Thus, ten roots of *Zea mays* (*everta*), in velocities ranging from 50^{cm} to 100^{cm} per minute, all attained an angle of 45° in 11 hours, and maintained the same angle to the end of the experiment, 10.5 hours later. *Helianthus annuus*, with ten roots in water flowing 100^{cm} to 500^{cm} per minute, showed all roots retaining their angle of 90°, 33 hours after the beginning of the experiment, this angle having been attained by most of the roots 15 to 18 hours earlier. Ten seedlings of *Raphanus sativus* (variety Yellow Oval) all bent their roots positively in a velocity of 350^{cm} to 400^{cm} per minute, temperature of water 23°, in a period between twelve and eighteen hours, the exact time not being observed. The angles attained varied from 15° to 90°. Thirty-six hours after beginning the experiment all roots were still positive, and at angles of 30° to 90°. A set of seven seedlings of the Early Long Scarlet radish held their positive angles to the close of the experiment, twenty-nine hours after the angles first appeared.

If the current is very weak many instances have been observed in which a root straightens into its vertical position after an incipient rheotropic curve. Four roots of *Avena sativa* growing in constant current velocities ranging from 50^{cm} to 100^{cm} per minute became positively rheotropic within the first 3¾ hours, but all straightened within the ensuing 1¼ hours. *Brassica alba* in one preparation in a revolving basin where the velocities for the roots ranged from 50^{cm} to 100^{cm} per minute showed six roots positive within three hours, but within the next hour four of these straightened. *Raphanus sativus*, during the first three hours of an experiment in which twelve seedlings were placed with their roots dipping into water, the velocities at the various distances from the center of the basin ranging from 50^{cm} to 100^{cm} per minute, and the water temperature being 22°, gave rheotropic responses in the three outermost roots. These roots after the lapse of four hours were seen to be straightening. Within the first seven hours of the experiment seven of the twelve roots bent positively, but after seven hours more, all twelve roots, except two tardily straightening ones, were in the vertical position, except for the fixed portions of the rheotropic curves.

Analyzing these results, it would seem that the matter can be thus stated: (1) a rheotropic curve in response to a weak stimulus will, sooner or later, be overcome by the response to gravitation, so that only the geotropic response is evident; (2) a stronger rheotropic stimulus acting at the same time with the normal geotropic stimulus may produce a curve giving a deviation of less than 90° from the vertical, this direction being regarded as a resultant of the water current stimulus and the gravitation stimulus; (3) with highly sensitive roots and a suitable rheotropic stimulus, an angle of 90° from the vertical may be attained, so that the geotropic response of the plant is wholly overcome by the rheotropic, except for the geotropic counter-curve which will be discussed later.

The overcoming of the response to one stimulus by that to another is well illustrated also in the horizontal position taken by stems in response to horizontally directed rays of light, where heliotropism apparently vanquishes geotropism.

V. THE GEOTROPIC COUNTER-CURVE.

One who studies the rheotropic behavior of roots soon notices that when a root has acquired an angle of great deviation from the vertical, the apical 2^{mm} of the root are bent downward, thus forming with the vertical a smaller angle than the part of the root farther back. If, for example, there is a rheotropic curve of 60°, the apex of the root will often show a downward dip of 5° to 40°. This appearance is well illustrated in *fig. 11*.

Both Berg (p. 27) and Juel (p. 529) have discussed this phenomenon, but neither, to my mind, in a very satisfactory manner. The former suggests that the apical 2^{mm} of the root may not be sensitive to the water stream stimulus, and hence this part does not take the direction of the growing zone, which Berg believes to be sensitive. The objection to the argument of Berg lies in the fact that it is not a question of sensitiveness but a question of response. The receptive tissue and the responsive tissue may be, we know, quite widely separated in various irritable phenomena. Juel explains the S-shaped curve formed by the rheotropic curve and the geotropic counter-curve as resulting from the competition of rheotropism and geotropism, the former being the stronger in the proximal part of the growing zone, and the latter being the stronger in the distal 2^{mm}.

Before proceeding with the discussion of the S-shaped curve, it may be well to state that it is not peculiar to rheotropism, but is seen also in heliotropism. If seedlings of *Brassica alba* be set up in the usual way with one-sided illumination, I have found when the heliotropic curve reaches or surpasses 45°, that the apical 2^{mm} show a geotropic counter-curve like that seen in rheotropism. If now, we take into account the experiments of Czapek[8] and Němec[9] showing that geotropic sensitiveness is most likely confined to the apical 1.5^{mm} to 2^{mm} of the root, and the experiments of Czapek[10] showing that roots receive their strongest geotropic stimulus when at an angle of 135° above their vertically downward position, and that the effect of the stimulus diminishes constantly with the reduction of this angle, we can readily see that the geotropic downward dip of a rheotropically curved root diminishes greatly the strength of the

[8] CZAPEK: Untersuchungen über Geotropismus. Jahrb. Wiss. Bot. **27**:243; **35**:313.

[9] NĚMEC: Ueber die Wahrnehmung des Schwerkraftreizes bei den Pflanzen. Jahrb. Wiss. Bot. **36**:78.

[10] CZAPEK: Jahrb. Wiss. Bot. **27**:283.

geotropic stimulus, and thus gives a greater opportunity for the operation of rheotropism. When a root is displaced out of its position of geotropic equilibrium, the angle of ensuing geotropic curvature has been observed by many to begin, according to the diameter of the root, 2^{mm} to 3^{mm} back from the apex. Roots, such as I have used for the most part, are 1.25^{mm} or less in diameter. In these, the geotropic angle is at first about 2^{mm} from the apex; subsequently the curve extends backward, and includes several more proximal millimeters. We may follow the formation of the S-shaped curve thus: The rheotropic curve begins in *Zea mays*, according to Berg, in the $3d^{mm}$ from the apex; and according to Juel in the $3d^{mm}$ of *Vicia sativa*. I have frequently seen it originate in the $2d^{mm}$ of both *Brassica alba* and *Raphanus sativus*, though in these plants it is often first seen in the $3d^{mm}$. Berg's, Juel's, and my own observations agree in noting that the counter-curve generally does not appear till the rheotropic curve has reached an angle approximating 45°. In one set of eight rheotropically curving roots of *Raphanus sativus*, seven had bent to 45° or over, and only one of these showed the dip of the tip. All these observations show that the tip of the root, even the apical 2^{mm}, may take a rheotropic curve. The part of the root farther back begins to curve a little later, and a portion removed as far as 11^{mm} from the apex, may, in *Zea mays*, according to Berg, participate in the rheotropic response. As the rheotropic angle increases, the sensitive apex of the root comes more and more into positions of increasing gravitation stimulus, till finally geotropism overcomes rheotropism, and the geotropic dip begins to appear. As soon, however, as the tip declines, the gravitation stimulus is less strongly felt and the rheotropic angle may now increase. This increase, however, is accomplished by farther bending several millimeters distant from the apex, the tip declining geotropically as the part behind it is lifted rheotropically. This behavior, after the S-curve begins to be formed, really implies a localization of the geotropic response and of the rheotropic response in different parts of the root. This fact is well worthy of special note, for by such initial geotropic curve the root is enabled to attain to a considerably greater rheotropic and heliotropic angle. The continuance of this behavior brings about a constant straightening of the geotropic curve in its proximal part and a constant re-formation of the geotropic curve in its distal part, giving in a root of *Raphanus sativus* that has been in its rheotropic and geotropic equilibrium for some hours, 2^{mm} to 3^{mm} of the apex dipping to an angle of 45° to 15° from the vertical, back of this apex a straight piece from several to many millimeters in length, generally lying at an angle of 45° to 90° above the vertically downward position, and lastly the rheotropic angle in the form of a more or less open arc connecting the rheotropically growing piece of the root with the older vertical part.

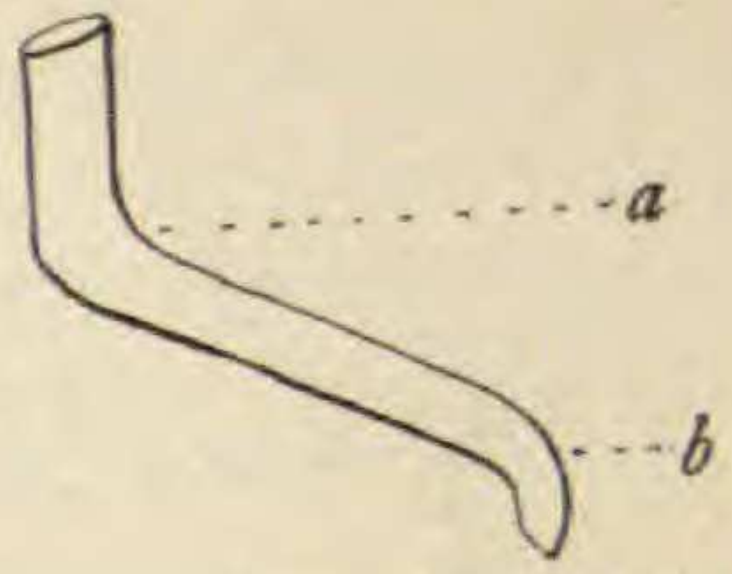

FIG. 11.— Root of *Lupinus albus*, showing (*a*) rheotropic curve and (*b*) geotropic counter-curve.

Fig. 11, drawn from a root of *Lupinus albus*, illustrates the features just described.

The rheotropic curve at the beginning may be quite like the geotropic curve of a root, but after some hours it will be noted

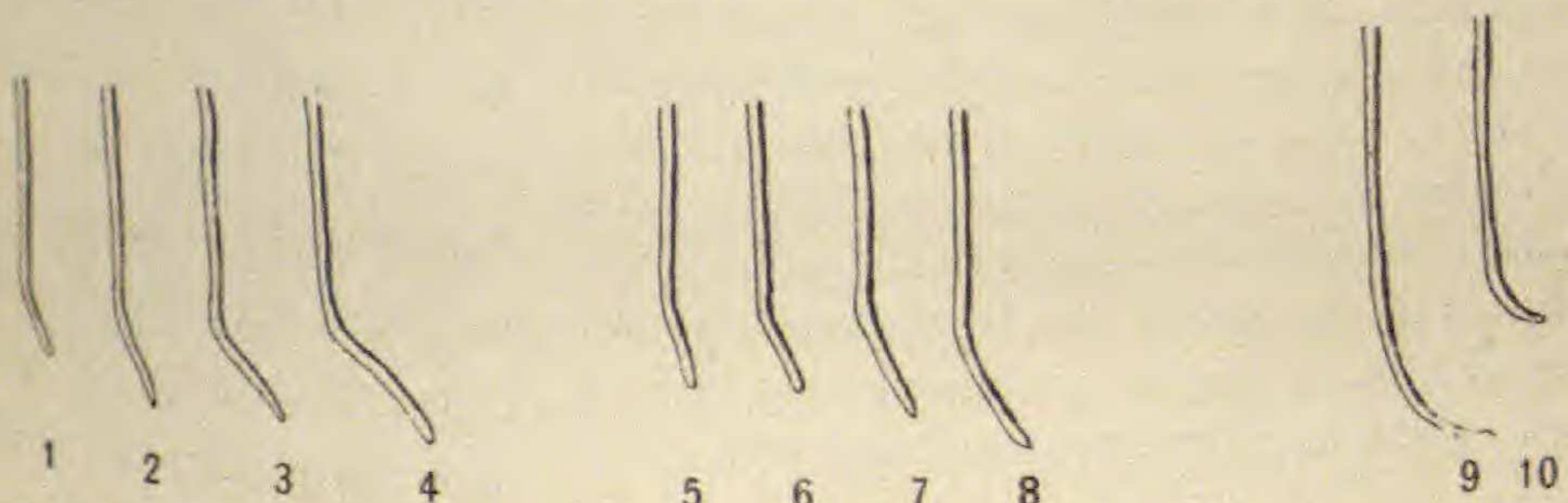

FIG. 12.—Numbers *1* to *4* are tracings of the rheotropic curves of a single seedling of *Raphanus sativus*, during the period of five hours. Numbers *5* to *8* are tracings of another root made at the same time. Numbers *9* and *10* show the geotropic curves of two roots of *Raphanus sativus*. The difference in the character of the rheotropic and the geotropic curves is apparent to the eye.

that the increase of the rheotropic curve is taking place by a bending farther back from the tip than occurs in a geotropic curve. *Fig. 12*, nos. *1* to *8*, shows rheotropic curves of two roots of *Raphanus sativus*, all made at the same time from the same variety and the same planting of seed. The roots were traced by laying them on ground glass under water, drawing on the ground glass with a lead pencil kept parallel with the roots, then transferring to paper by laying the paper over the ground glass set in a window. *Fig. 12*, nos. *9* and *10*, shows geotropic curves after the plants had been lying horizontally for four hours, with roots in water at a temperature of 23°. The rheotropic curves of *1* to *4* were made in velocities of water ranging from 100^{cm} to 400^{cm} per minute, temperature of water being 22°; and the curves of *5* to *8* were made in similar circumstances except that the velocities ranged from 150^{cm} to 600^{cm} per minute. The early rheotropic curve of 32° at 3^{mm} from the apex in no. *1* continued to increase by farther bending in the same tissue even when this had become 5^{mm} to 6^{mm} distant from the apex, till in no. *4* the angle had become 43°. So also in the roots numbered *5* to *8*, it is evident from the figures that the initial bending of 15° at 3^{mm} from the apex in *5* has in *8* increased to 32° by farther bending in the same tissue, though in the latter case the apex of the angle is 6^{mm} from the root-tip.

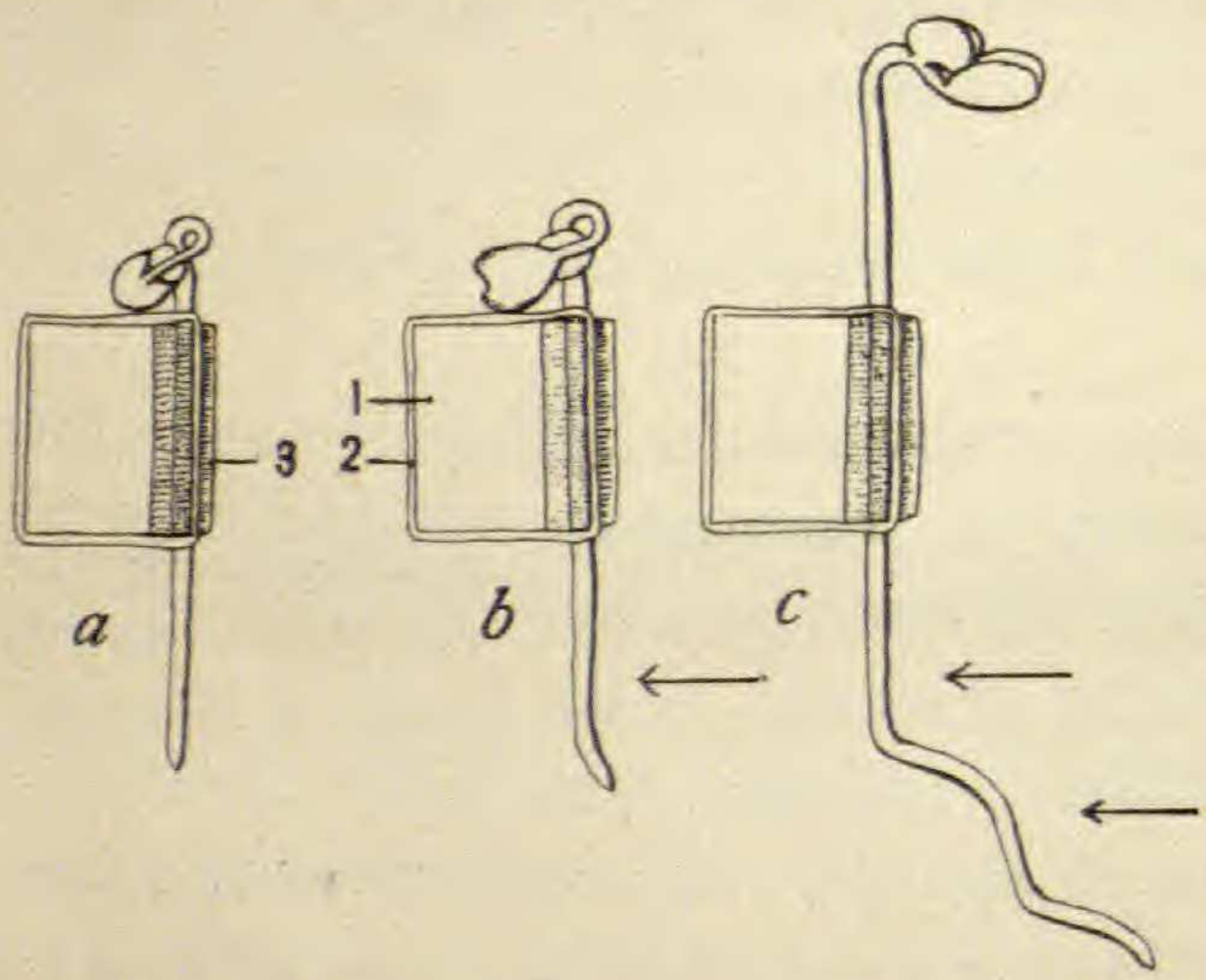

FIG. 13.—*Raphanus sativus.* Three stages of a single seedling illustrating the undulating course of the root; selected from a single preparation of 16 seedlings, 12 of which had similar curves; *a* shows the seedling before beginning the revolution of the basin of water; *b*, after three hours' revolution; *c*, after 21 hours' revolution. The number *1* represents the end of the supporting bar of wood; *2*, the rubber bands holding the two strips of blotting paper (*3*) against the bar of wood. The temperature was 23.5° in water.

A singular result worthy of note is the appearance in a root of several alternating curves of greater and of lesser angle, giving to the root an undulating course. This is well illustrated in *fig. 13*, where a root shows two greater angles and two lesser. This phenomenon I have seen only in two conditions—in high temperatures when the growth was very rapid, and with a very weak stimulus, the latter illustrated in *fig. 8, c.* It may be explained in either of two ways. We may suppose that the root changes its sensitiveness or degree of response in successive periods of time; or we may suppose that the after-effect of the gravitation stimulus on the one hand, and of the rheotropic stimulus on the other alternately carries the bending root beyond the position of equilibrium, thus producing an oscillation back and forth over the position of equilibrium, the older part of the curving portion being fixed at the two extremes of position, thus producing the undulation observed. That a root may become non-responsive to a water stream after it has already given a rheotropic curve has been shown above. No observations have shown that such a root may in the same current of water show a second response. If, however, a root may regain its sensitiveness or its ability to respond after losing the same, we might expect the appearance of such an undulating course in growth as that just described.

[*To be concluded.*]